EVALUATION OF HARVEST STRATEGIES FOR TANNER CRAB STOCKS THAT EXHIBIT PERIODIC RECRUITMENT

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ABSTRACT Recruitment to most Tanner crab (*Chionoecetes bairdi*) stocks in Alaska is periodic, causing wide fluctuations in population abundance. We evaluated alternative management approaches for such Tanner crab stocks with a size-based computer simulation model. Our study focused on Bristol Bay Tanner crab, the largest Tanner crab stock in Alaska, for which a stock–recruitment relationship with recruitment periodicity has been estimated. Alternative management approaches include a 40% harvest rate on legal males (status quo), variable harvest rates based on reproductive biomass, and strategies based on mature abundance, gear selectivity, and shell condition. Under the apparent recruitment periodicity of 10–18 years, maximum mean yield is achieved with a legal harvest rate >60% with large variation in yield and a high probability of fishery closure. Because of weak density dependence, the yield curve is relatively insensitive to high harvest rates. No harvest strategies can prevent stock collapse when recruitment has long periodicity and high amplitude, although a conservative strategy reduces the probability of stock collapse. We propose a harvest strategy for Bristol Bay Tanner crab that is 0, 10%, or 20% of molting mature males when effective reproductive biomass is $<7{,}030$ t, $\ge 7{,}030$ and $<15{,}400$ t, or $\ge 15{,}400$ t, respectively, with a 50% cap on harvest rate for exploitable legal crabs. The proposed strategy adjusts legal harvest rates according to changes in stock productivity indexed by recruitment strength: high legal harvest rates during the upward recruitment cycle and low rates that protect large-size crabs and reproductive potential during the downward recruitment cycle. As compared to the status quo harvest strategy, the new approach is easily implemented, has similar tradeoffs between high mean yield and relatively low variation in yield, while reducing shortages of mates for mature females and increasing fishing opportunities.

KEY WORDS: Tanner crab, *Chionoecetes bairdi*, periodic recruitment, harvest strategies, fisheries management, Alaska

INTRODUCTION

Tanner crab (*Chionoecetes bairdi*) are widely distributed in the waters off Alaska, extending as far north as Norton Sound and as far south as Southeast Alaska. The stocks used to support some of the most important fisheries in Alaska. The fisheries have followed a boom and bust cycle. In the eastern Bering Sea, Tanner crab were first targeted by Japanese and Russian fleets in 1965. The eastern Bering Sea fishery expanded quickly in the late 1960s, and the catch reached 24,000 t in 1968. Foreign fishing for Tanner crab has been prohibited under the Magnuson Fisheries Conservation and Management Act since 1980. Directed fisheries for eastern Bering Sea Tanner crab by the U.S. fleet began in 1974. Catch peaked in 1978 at 31,300 t (Otto 1990). The population collapsed in the mid-1980s, and no fishing was allowed in 1986 and 1987. During 1990 to 1993, catches averaged 15,000 t and annual ex-vessel values averaged US$46 million. Catches dropped sharply after 1993, and the eastern Bering Sea fishery has been closed since 1997 because of the depressed stock condition. Most other Tanner crab fisheries in Alaska collapsed in the early to mid-1990s, and none of the depressed stocks have recovered.

Wide fluctuations in catches are caused by fluctuations in population abundance for which highly variable recruitment dynamics are responsible. Like many fish stocks (Koslow 1989), recruitment to most Tanner crab stocks in Alaska is periodic and strongly autocorrelated (Zheng and Kruse in press). Recruitment to the Bristol Bay stock was strong in the mid-1970s and late and early 1990s and weak during the mid-1980s and mid- and late 1990s; recruitment to the northern Gulf of Alaska stocks was strong in the mid-1970s and has been weak since the early 1990s (Zheng and Kruse in press). Although recruitment is likely to result from a combination of density-dependent and density-independent factors, it is difficult to separate the effects of density-dependent

reproductive stock and autocorrelated environmental factors, as is typically the case (Deriso et al. 1986; Walters and Collie 1988). To date, stock–recruitment (S–R) relationships have been estimated only for Bristol Bay Tanner crab in the eastern Bering Sea (Zheng and Kruse 1998). For this stock, reproductive biomass explained only a small portion of recruitment variability, and residuals from the fitted S–R curve showed a strong cyclic trend (Zheng and Kruse 1998).

Currently, Tanner crab fisheries in Alaska are managed by a size/sex/season approach; that is, harvest of only large males and no fishing during spring molting and mating periods. The size/sex/season approach is based on economic consideration of market value and meat yield, protection of females for reproduction, and allowance of at least one mating season for males. In addition, commercial removals from assessed populations are based on a constant harvest rate strategy when abundance estimates are available. For example, for the eastern Bering Sea stock, a harvest rate of 40% is applied to the abundance of legal-sized male crabs (>137 mm carapace width, CW). Optimal harvest rates have not formally been evaluated for any Tanner crab stock in Alaska. Fishery thresholds have not been established and evaluated either, despite the fact that many Tanner fisheries in Alaska are currently closed because of the depressed stocks. In 1999, the U.S. Secretary of Commerce ruled that Tanner crab were overfished in the eastern Bering Sea.

National Standard 1 of the Magnuson–Stevens Fishery Conservation and Management Act requires that "conservation and management measures shall prevent overfishing while achieving, on a continuous basis, the optimal yield from each fishery . . ." (NMFS 1996). For a Tanner crab stock exhibiting a strong periodic and autocorrelated recruitment pattern, what is the optimal harvest strategy to produce relatively high yield, low variation in yield, and minimum chance of stock collapses? Although harvest strat-

egies for fish stocks with such recruitment patterns have been evaluated (e.g., Koslow 1989; Parma 1990; Walters and Parma 1995), no such studies have been conducted for Tanner crab stocks. In this study, we constructed a size-based model, based on crab CW, to facilitate a computer simulation analysis of alternative harvest strategies for Tanner crab stocks that exhibit periodic recruitment. Our study focused on Bristol Bay Tanner crab, the largest Tanner crab stock in Alaska. Alternative harvest strategies include a 40% harvest rate on legal males (status quo), variable harvest rates based on reproductive biomass, and strategies based on mature abundance, gear selectivity, and shell condition.

METHODS

Population Model and Parameters

The size-based population model constructed by Zheng et al. (1998) for Bristol Bay Tanner crab was used in this study and is summarized in the Appendix. We set the minimum CW at 93 mm for males and 70 mm for females and simulated crab abundance using width class intervals of 5 mm. The last width class included males ≥163 mm CW and females ≥115 mm CW. Population parameters from Zheng et al. (1998) were updated using data from 1975 to 1997 and are summarized in Table 1. Population abundances were simulated for June each year, after crabs have generally completed annual molting and mating. Because fishing usually occurred during November each year since 1993, we used a lag of 0.4 year between the abundance assessment and the November fishery in our simulations.

A constant natural mortality was used in our simulations. Handling mortality from the other crab fisheries was part of natural mortality. Handling mortality from the directed Tanner crab fishery and bycatch mortality from all nonpot fisheries were separated from natural mortality. Therefore, natural mortalities for both males and females were lower than those estimated by the size-based model of Zheng et al. (1998), in which all handling mortality was included in the estimates of natural mortality. To examine sensitivity of the alternative strategies to levels of natural mortality, we compared evaluation criteria for low natural mortality and high natural mortality represented by 62.5% and 137.5% of the baseline natural mortalities (Table 1).

The level of handling mortality from the directed pot fishery was determined by gear selectivities of sublegal males and females and handling mortality rate. We estimated the gear selectivities of sublegal male and mature female crabs from the observer data from 1990 to 1996 (Table 1) and assumed a 20% handling mortality rate for those crabs that are caught and returned to the sea (Zheng et al. 1998). To investigate sensitivity of results to handling mortality rate, we also simulated scenarios with 0% and 50% handling mortality rates that bracket the range of likely values.

Bycatches were estimated for two kinds of nonpot fisheries: scallop and groundfish. Annual Tanner crab bycatch from the eastern Bering Sea scallop fishery was assumed to equal the modeled population abundance times the current bycatch limitation rate of 0.1354% (J. Barnhart, Alaska Dept. of Fish and Game, Kodiak, Alaska, pers. comm.). The current limit of Tanner crabs in the eastern Bering Sea groundfish fisheries was a step function of total Tanner crab abundance estimated from the survey and was separately set for two zones (Witherell 1997). Zone 1 and part of Zone 2 are in Bristol Bay. The abundance of the modeled Bristol Bay population was about 40% of the total surveyed abundance of the

eastern Bering Sea from 1988 to 1997; so, all bycatch limits for the groundfish fisheries were multiplied by 0.4 in the simulations. In addition, all bycatch limits from Zone 2 were also multiplied by 0.89, because an average of 89% of the observed bycatch in Zone 2 came from Bristol Bay from 1993 to 1997. The bycatch in Zone 2 rarely exceeded the limits; therefore, we set the maximum bycatch limit for the modeled population from the groundfish fisheries in the Bristol Bay area of Zone 2 as 0.748 million of crabs (2.1*0.4*0.89) (Witherell 1997). Mortality rates for Tanner crab bycatches from the scallop fishery and groundfish fisheries were assumed as 40% and 80%, respectively (NPFMC 1996).

Survey measurement error was assumed to follow a lognormal distribution. Simulated "true" values of effective reproductive biomass and crab abundance were multiplied by a measurement error to mimic the survey estimation process for each year. Effective reproductive biomass was defined as biomass of females >79 mm CW that can be mated by mature males (Zheng and Kruse 1998). The lognormal measurement errors were simulated with a standard deviation of 0.2 and a mean of zero. To prevent extremely large errors in estimated values of abundance, both ends of the measurement-error distribution were truncated to fall within its 98% confidence limits.

S–R data for Bristol Bay Tanner crab were fitted to a normal Ricker model by Zheng and Kruse (1998), and this S–R relationship with cyclic residuals from a sine function was used to conduct our simulations (Fig. 1). Sensitivity of the harvest strategies to depensation was also examined by using a depensatory Ricker S–R curve with cyclic residuals. Sex ratio of recruits was assumed to be 55% males and 45% females based on the average ratio of recruitment estimates from 1976 to 1997 (Zheng et al. 1998). A lower proportion of female recruits is likely caused by a lower catchability by the trawl survey gear. The period length of recruitment cycles was randomly set from 10 to 18 years. Sensitivities to cycle period length and amplitude were investigated by varying cycle period length from 4 to 30 years and cycle amplitude from 0.4 to 2.5.

Molting probabilities for males and maturity probabilities for females varied over time (Zheng et al. 1998). Although these probabilities were not strongly correlated with recruitment strengths, periods with higher molting probabilities for males and lower maturity probabilities for a given size for females generally occurred during good recruitment periods. To incorporate this dynamic feature into the simulation model, we used two molting probability functions for males and two maturity functions for females based on the updated results by Zheng et al. (1998). The high molting probability function was used during periods with upward recruitment cycles whereas the low molting probability function was used during periods with downward recruitment cycles. Only a few years occurred when the 50% maturity for females were at large sizes (Zheng and Kruse 1998); thus, the low maturity probability function (becoming mature at large size) was used only during periods with the highest 50% of upward cycles. The high maturity probability function was used during the rest of a recruitment cycle.

Alternative Strategies

In this study, we examined three kinds of alternative harvest strategies to set guideline harvest levels (GHL; i.e., annual catch quotas). These approaches ranged from a simple approach to a

TABLE 1.

Population parameters for a size-based model of Bristol Bay Tanner crab updated from Zheng et al. (1998). "New" and "Old" refer to shell condition of crabs.

Male Crabs

Mid-CW (mm)	Weight (Kg)	Initial Abund.		Molting Probability				Selectivity	
		New	Old	New		Old		New	Old
		(million)		High	Low	High	Low		
95.5	0.260	1.202	0.613	0.944	0.827	0.136	0.000	0.104	0.057
100.5	0.304	1.449	0.975	0.922	0.777	0.136	0.000	0.103	0.056
105.5	0.354	1.371	1.201	0.893	0.717	0.136	0.000	0.164	0.057
110.5	0.408	1.070	1.295	0.855	0.648	0.136	0.000	0.311	0.099
115.5	0.468	0.780	1.643	0.805	0.572	0.136	0.000	0.333	0.123
120.5	0.534	0.554	2.100	0.745	0.491	0.136	0.000	0.488	0.126
125.5	0.606	0.366	2.233	0.673	0.410	0.136	0.000	0.706	0.139
130.5	0.684	0.175	1.994	0.592	0.332	0.136	0.000	0.958	0.201
135.5	0.768	0.118	1.893	0.506	0.261	0.136	0.000	1.000	0.220
140.5	0.860	0.071	0.884	0.420	0.200	0.136	0.000	1.000	0.317
145.5	0.958	0.039	0.590	0.338	0.150	0.136	0.000	1.000	0.317
150.5	1.064	0.019	0.398	0.265	0.111	0.136	0.000	1.000	0.317
155.5	1.177	0.008	0.242	0.203	0.080	0.136	0.000	1.000	0.317
160.5	1.298	0.003	0.145	0.152	0.058	0.136	0.000	1.000	0.317
165.5	1.428	0.000	0.204	0.113	0.041	0.136	0.000	1.000	0.317

Female Crabs

Mid-CW (mm)	Weight (Kg)	Initial Abund.		Mature Probability		Selectivity	
		New	Old	Low	High	New	Old
72.5	0.215	1.359	2.158	0.024	0.368	0.007	0.030
77.5	0.256	1.520	2.816	0.056	0.488	0.024	0.042
82.5	0.300	1.255	2.893	0.126	0.632	0.059	0.080
87.5	0.349	0.842	2.822	0.260	0.768	0.170	0.102
92.5	0.402	0.476	2.409	0.462	0.867	0.323	0.142
97.5	0.461	0.227	1.624	0.677	0.928	0.333	0.205
102.5	0.524	0.091	0.873	0.837	0.961	0.333	0.359
107.5	0.592	0.021	0.335	0.926	0.978	0.333	0.359
112.5	0.665	0.007	0.115	0.968	0.987	0.333	0.359
117.5	0.743	0.003	0.043	0.987	0.992	0.333	0.359

Growth			Natural Mortality			S-R Models				Prop. by Width		
Para	Male	Female	Level	Male	Female	Para	Normal	Para	Depensa	Para	Male	Female
a	15.75	25.60	mean	0.40	0.43	α	2.0402	κ	0.2031	α_r	100.0	80.67
b	0.070	−0.134	low	0.25	0.27	β	0.0563	θ	2.8031	β_r	1.023	0.955
β	0.746	1.000	high	0.55	0.59	A	1.2676					
						P	10–18 yrs					
						σ	0.4570					

more complex approach incorporating gear selectivity and shell condition. Under the first harvest strategy, the status quo, GHL was set by legal harvest rate multiplied by legal male crab abundance. The current legal harvest rate is 40%, but we also evaluated nine other rates ranging from 10% to 60%. Under the second alternative, GHL was set by legal harvest rate multiplied by "exploitable" legal male crab abundance. Because the fishery disproportionately harvests new-shell crabs over old-shell crabs, we defined exploitable legal males based on fishery selectivity parameters. We estimated 100% selectivity for new-shell crabs and 32% selectivity for old-shell crabs based on comparison of catch and survey data from 1975 to 1997. Ten alternative harvest rates for exploitable legal males ranging from 15% to 65% were evaluated. Under the third approach, GHL was set by mature harvest rate multiplied by "molting mature males," but only legal males were allowed to be harvested with a catch cap of 50% of exploitable legal male abundance. In other words, the legal harvest rate is equal to the mature harvest rate multiplied by "molting mature male" abundance divided by legal male abundance. "Molting mature males" were defined as 100% of new-shell males and 15% of old-shell males >112 mm CW. These mature males have a high probability of molting within a year. Ten alternative mature harvest rates ranging from 10% to 35% were evaluated.

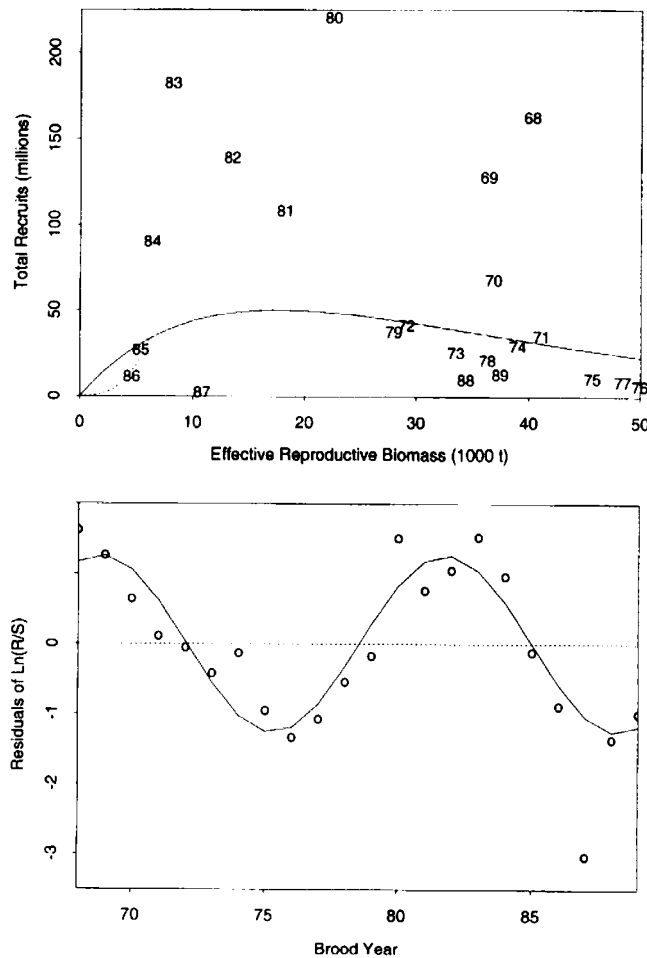Because the S–R relationship is weakly density dependent, we

Figure 1. Relationships between effective reproductive biomass (S) and total recruits at age 7 (i.e., 8-year time lag, upper plot) and residuals of logarithm of recruits per S from a normal Ricker curve (lower plot) for Bristol Bay Tanner crab. In the upper plot, numerical labels are brood year, solid line is a normal Ricker curve without autocorrelated component, and dotted line is an exponential S-R curve (depensatory curve). In the lower plot, open circles represent residuals estimated from deviations of S-R datapoints from the normal Ricker curve, and solid line represents residuals fitted to a sine function.

did not attempt to estimate an optimal threshold in our simulations. Rather, we set a threshold based partly on past fishery management practice and partly on the S-R relationship. In the past, the effective reproductive biomass was always below 7,030.0 t in the years when the fishery was closed. This level of effective reproductive biomass is slightly above the smallest effective reproductive biomass with an above average recruitment level (Fig. 1).

A stair-step harvest rate schedule similar to that employed for the Bristol Bay red king crab (*Paralithodes camtschaticus*) fishery (Zheng et al. 1997) was also evaluated for each approach. We used 22,000 t of effective reproductive biomass as a base level, which is the average of simulated effective reproductive biomass under the status quo constant 40% legal harvest rate. When effective reproductive biomass was at or below 50%, 60%, or 70% of this base level, harvest rates would decrease by 50% or 40%. A combination of three levels of effective reproductive biomass and two levels of reduced harvest rates resulted in six alternative stair-step harvest rate schedules. We evaluated each stair-step schedule in combination with each of the three harvest strategy approaches.

Simulations

The alternative harvest strategies were evaluated by simulating the Bristol Bay Tanner crab stock and fishery with the population dynamic model and a standard set of population parameters. The simulation model was initialized with effective reproductive biomass from 1990 to 1997 (Zheng and Kruse 1998) and population abundance in 1997 (Table 1) so that year 1 corresponded to 1998. The simulated time horizon was set at 100 years. Each scenario was replicated 1000 times to ensure relative stability of statistics. Identical seeds for random number generators were used for all scenarios to compare different strategies under identical environmental conditions.

We examined sensitivity of each strategy to changes in natural mortality, handling mortality, and S-R curve. The standard set of population parameters was used in each sensitivity analysis, except that both a normal Ricker S-R curve and depensatory S-R curve were used and that the parameter under consideration was assigned one of two opposite and extreme values. For sensitivity studies on recruitment cycles, we used 200 replicates, each for 1000 years. A longer simulated time horizon was needed to examine cycle period length.

To evaluate the strategies, statistics were collected on effective reproductive biomass, probabilities of fishery closure, probabilities that the stock is below the overfished reference point as defined in the fishery management plan (NPFMC 1998), and yield. Probabilities of fishery closure are denoted as the proportions of replicates with estimated effective reproductive biomass below threshold so that the fishery is prohibited for a given year. The overfished level is defined for Tanner crab in the entire eastern Bering Sea, not just Bristol Bay. Based on the survey data from 1983 to 1997, we approximated the equivalent overfished level for Bristol Bay Tanner crab as 26,600 t of total mature male and female biomass. Results were averaged over the simulated time horizon and over all replicates. To assess optimality, an equal tradeoff value between increase in mean yield and decrease in standard deviation of yield was computed as 0.5*yield−0.5*standard deviation (Zheng et al. 1997) for each alternative strategy.

RESULTS

The tradeoff between mean yield and standard deviation of yield as a function of constant harvest rate (i.e., without the stair-step) was similar among the three approaches (Fig. 2). Mean yield, standard deviation of yield, and proportion of years that mature population abundance was below the overfished reference point increased as a function of harvest rate, but the standard deviation increased at a faster rate than mean yield. The rate of increase in mean yield generally slowed down as harvest rate increased, especially with legal harvest rate >40%, exploitable harvest rate >45%, and mature harvest rate >20%. Variations in yield, indexed by standard deviations of yield, were very high for all three approaches. This is a direct result of the periodic recruitment feature of Tanner crab population dynamics. Even without a fishery, reproductive biomass fell below the overfished reference point in 9.4% of years. The legal harvest rate of 40% (status quo) is equivalent to an exploitable legal harvest rate of 45% and a mature harvest rate of 20%. Under equivalent harvest rates, both legal harvest rate and exploitable legal harvest rate approaches had similar mean yield and standard deviation of yield, but the proportion of years at overfished levels was lower for the exploitable harvest rate approach than the harvest rate approach. Mean yield, standard
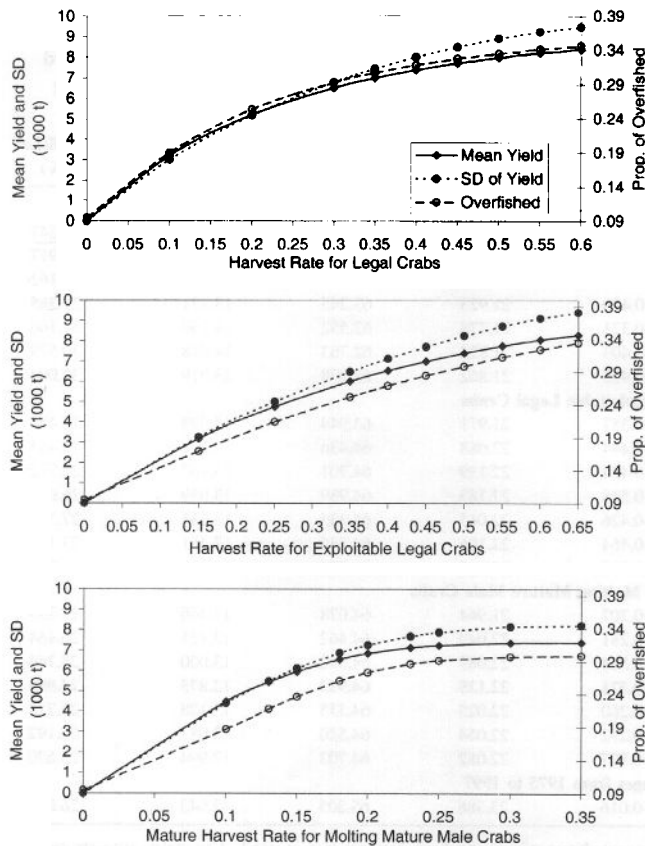
Figure 2. Mean yield (solid lines), standard deviation of yield (dotted lines), and probability of being at overfished levels (dashed lines) as a function of constant harvest rate for Bristol Bay Tanner crab under the normal S–R curve and a 20% handling mortality rate. In the top, middle, and lower plots, harvest rates apply to total legal crabs, exploitable legal crabs, and molting mature male crabs, respectively.

deviation of yield, and proportion of years at overfished levels with the 20% mature harvest rate approach were the lowest among the three equivalent approaches. The 50% cap on exploitable harvest rate for the mature harvest rate approach resulted in relatively flat curves of mean yield, standard deviation, and proportions of years at overfished levels when mature harvest rates were high (Fig. 2).

Alternative stair-step functions of harvest rate generally did not change the results very much (Table 2). Because standard deviation of yield increased much faster than mean yield at legal harvest rate >40%, exploitable legal harvest rate >45%, and mature harvest rate >20% (Fig. 2), we used these harvest rates as the high harvest rate levels in the stair-step functions. The legal harvest rate of 40% also happens to be the status quo harvest rate. For each approach, a decrease from 70 to 60 to 50% in cut-off levels of effective reproductive biomass or an increase in low harvest rates from 50 to 60% resulted in slightly higher trade-off values between increase in mean yield and decrease in standard deviation of yield but caused slightly higher percentages of years with fishery closure and with mature biomass being below the overfished reference point (Table 2). Overall, the mature harvest rate approach had slightly higher trade-off values between increase in mean yield and decrease in standard deviation of yield compared to the other two approaches. It also had slightly lower percentages of years with fishery closure and fewer years being overfished. The harvest strategy with a high mature harvest rate of 20% and a low rate of 10%

with a cut-off of 15,400 t of effective reproductive biomass had the lowest percentages of years with fishery closure and at overfished levels among all the alternatives (Table 2). The trade-off value between increase in mean yield and decrease in standard deviation of yield was intermediate among the range in values among all harvest strategies (Table 2). In the context of National Standard 1, we considered this strategy as the most attractive alternative to the status quo strategy.

Sensitivity analyses of natural mortality, handling mortality, S–R curve, and recruitment cycle were conducted on the proposed new strategy and the status quo strategy. As expected, higher natural mortality or handling mortality rate resulted in much lower catch and higher percentages of years with fishery closure and at overfished levels for all alternative strategies (Table 3), and vice versa for lower natural mortality or handling mortality rate. The depensatory S–R curve had a minor effect on the results of simulations except when depensation was combined with high natural mortality, which resulted in extremely low population abundances and few fishing opportunities (Table 3). Effective reproductive biomass rarely fell into the depensatory range under other circumstances.

Under the same conditions, the status quo harvest strategy had slightly higher mean yield, lower standard deviation of yield, higher percentages of years with fishery closure and at overfished levels than when the status quo harvest strategy included stair-step harvest rates (Table 3). The status quo harvest strategy also had higher mean yields than those for the proposed new strategy under the same conditions, but its standard deviations of yield and its percentages of years at overfished levels were much higher (Table 3).

With the normal S–R curve, the status quo and proposed harvest strategies were very sensitive to period length and amplitude of recruitment cycle, especially for a long period length and high amplitude (Fig. 3). Coefficient of variation of yield and proportions of years of fishery closure and at overfished levels increased substantially as period length and amplitude of recruitment cycle increased. For a given combination of period length and amplitude of recruitment cycle, the proposed harvest strategy resulted in only a minor improvement on coefficient of variation of yield and proportion of years of fishery closure over the status quo strategy (Fig. 3). The proposed harvest strategy reduced proportions of years at overfished levels considerably when the recruitment cycle period length was 18 years or less.

The sensitivities of the status quo and suggested harvest strategies to the depensatory S–R curve depended on period length and amplitude of recruitment cycle (Fig. 4). For a period length ≤10 years or an amplitude ≤1.0, effective reproductive biomass rarely fell below the depensatory range; thus, the simulation results between the normal S–R curve and the depensatory S–R curve were almost identical for this region of parameter values (Figs. 3, 4). For combinations of period lengths ≥15 years and amplitudes ≥1.5, coefficients of variation of yield and proportions of years of fishery closure and years at overfished levels were much higher with the depensatory S–R curve than with the normal S–R curve (Figs. 3, 4). For combinations of extremely long period length and high amplitude, effective reproductive biomass with the depensatory S–R curve was always below the threshold level (Fig. 4). Under likely ranges of 10–18 years of period length and amplitudes of 1.0–1.4, the depensatory S–R curve did not have a major impact on the simulation results. Similar to the results with the normal S–R curve, the proposed new harvest strategy reduced proportions of

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TABLE 2.

Comparisons of mean yield, standard deviation of yield (SD), equal trade-off between increase in mean yield and decrease in standard deviation of yield, mean effective reproductive biomass (SP), mean total mature biomass (TMB), percentage of years without fishing (Closure), and percentage of years below the overfished reference point (Overfished) for alternative harvest strategies.

Cut-off (1000 t)	High HR	Low HR	Yield (1000 t)	SD (1000 t)	Tradeoff	SP (1000 t)	TMB (1000 t)	Closure (%)	Overfished (%)
				Harvest Rates Applied to Total Legal Crabs					
7.030	0.400	0.000	7.377	7.999	−0.311	21.660	62.133	14.521	31.847
11.000	0.400	0.200	7.313	8.095	−0.391	21.812	62.676	14.034	30.917
13.200	0.400	0.200	7.267	8.138	−0.435	21.872	62.957	13.848	30.162
15.400	0.400	0.200	7.211	8.170	−0.480	21.923	63.245	13.721	29.385
11.000	0.400	0.240	7.328	8.071	−0.371	21.778	62.552	14.150	31.146
13.200	0.400	0.240	7.294	8.101	−0.403	21.824	62.763	14.018	30.579
15.400	0.400	0.240	7.253	8.122	−0.435	21.862	62.978	13.919	30.004
				Harvest Rates Applied to Exploitable Legal Crabs					
7.030	0.450	0.000	6.988	7.702	−0.357	21.971	63.944	13.598	28.480
11.000	0.450	0.225	6.912	7.801	−0.444	22.088	64.436	13.291	27.483
13.200	0.450	0.225	6.862	7.851	−0.494	22.139	64.701	13.167	26.772
15.400	0.450	0.225	6.800	7.895	−0.548	22.185	64.989	13.059	26.019
11.000	0.450	0.270	6.928	7.780	−0.426	22.065	64.335	13.351	27.706
13.200	0.450	0.270	6.889	7.818	−0.464	22.106	64.545	13.251	27.122
15.400	0.450	0.270	6.841	7.850	−0.505	22.143	64.772	13.158	26.524
				Mature Harvest Rates Applied to Molting Mature Male Crabs					
7.030	0.200	0.000	6.844	7.258	−0.207	21.964	64.078	13.366	27.333
11.000	0.200	0.100	6.778	7.339	−0.281	22.049	64.462	13.121	26.464
13.200	0.200	0.100	6.732	7.381	−0.324	22.089	64.682	13.000	25.754
15.400	**0.200**	**0.100**	**6.676**	**7.418**	**−0.371**	**22.125**	**64.922**	**12.875**	**24.986**
11.000	0.200	0.120	6.796	7.316	−0.260	22.025	64.355	13.188	26.714
13.200	0.200	0.120	6.761	7.346	−0.292	22.054	64.520	13.087	26.192
15.400	0.200	0.120	6.718	7.372	−0.327	22.082	64.703	12.994	25.620
				Estimated Historical Averages from 1975 to 1997					
			6.813	6.846	−0.016	23.586	65.205	13.043	26.087

"Cut-off" is a level of SP below which the low harvest rate (HR) is used and at or above which the high harvest rate is used. The status quo strategy is underlined and the proposed new strategy is shown in bold. Historical data were included for comparison.

years of fishery closure and at overfished levels considerably when period length of recruitment cycle was 18 years or less and amplitude was 1.8 or less (Fig. 4).

Although the status quo harvest strategy is a constant legal harvest rate of 40%, legal harvest rates actually implemented during the last 23 years were quite different from this level and varied greatly over time (Fig. 5). Realized legal harvest rates were higher than 40% during 1977 to 1980 and 1989 to1992 and much lower during 1983 to 1988 and 1994 to1997. It seems that it is difficult to implement a constant legal harvest rate strategy. Preseason GHLs were generally slightly higher than actual yields for most years but much higher than actual yields when the GHLs were low (Fig. 5). The proposed harvest strategy leads to higher legal harvest rates than the historical rates of the status quo strategy when population abundance is increasing and to lower rates when population abundance is decreasing. Historical harvest rates more closely match the proposed new harvest strategy than the status quo "constant" harvest rate strategy (Fig. 5).

DISCUSSION

Changing environments pose great challenges to fishery managers. Environmental shifts cause large changes in growth, mortality, and recruitment, making it difficult to design, evaluate, and implement optimal harvest strategies that are robust to wide swings in productivity. When trends in environmental effects on recruitment can be predicted, harvest strategies can be adjusted to maximize expected discounted yield. Escapement goals (Parma 1990) or harvest rates (Criddle et al. 1998) can be raised when

favorable conditions are anticipated and lowered when poor conditions are expected. Even lacking knowledge of environmental effects, a constant harvest rate strategy still produces a long-term harvest close to the theoretical optimum for stocks with periodic or autocorrelated recruitment (Walters and Parma 1995). However, neither constant harvest rate nor escapement goal strategies can prevent collapse of stocks with high-amplitude, low-frequency recruitment variability, although a constant escapement strategy minimizes the risk (Koslow 1989).

Harvest strategies for Tanner crab differ from those for many fish stocks, because they take into account differences in biology. Female Tanner crabs can store sperm for more than 1 year, and stored sperm from multiple matings may fertilize clutches for the subsequent 2 years (Paul 1984). A mature male Tanner crab can mate with a maximum of 8–10 females in a laboratory setting during a breeding season (Paul 1984), although the number of females a male can mate in the field may be less than this maximum number because of low density or discrete spatial distributions of the sexes and a limited mating window. Conceivably, the size/sex/season approach coupled with a suitable harvest rate on legal crabs of size one or two molts larger than mature males could adequately protect reproductive potential of Tanner crab. However, molting probabilities of male crabs decrease sharply when they attain large claws (unpublished data), and periods of poor recruitment lead to depressed populations predominated by old "skip molt" or "terminal molt" crabs. Applying a constant harvest rate to total legal abundance when the abundance is low could result in a high discard rate of old-shell crabs and a very high

TABLE 3.

Comparisons of mean yield, standard deviation of yield (SD), mean effective reproductive biomass (SP), mean total mature biomass (TMB), percentage of years without fishing (Closure), and percentage of years below the overfished reference point (Overfished) for three harvest strategies under low and high natural mortality (M), three levels of handling mortality (HM) and two S–R curves for the status quo, modified status quo, and proposed new strategy (see Table 2).

Harvest Strategy	M	HM	Yield (1000 t)	SD (1000 t)	SP (1000 t)	TMB (1000 t)	Closure (%)	Overfished (%)
Normal S–R Curve and Harvest Rates Applied to Total Legal Crabs								
Status quo	Low	0.2	11.080	12.157	33.494	89.759	2.26	13.92
Status quo	High	0.2	4.226	4.837	13.709	41.418	33.55	43.45
Status quo	Normal	0.0	8.213	8.933	23.675	67.118	11.81	28.84
Status quo	Normal	0.5	6.172	6.687	19.000	55.236	18.43	35.65
Modif. status quo	Low	0.2	11.046	12.227	33.673	90.272	2.15	12.44
Modif. status quo	High	0.2	3.857	4.841	13.923	42.721	32.88	40.90
Modif. status quo	Normal	0.0	8.004	9.067	23.682	67.632	11.78	27.05
Modif. status quo	Normal	0.5	6.077	6.895	19.614	57.198	16.44	32.48
Normal S–R Curve and Harvest Rates Applied to Molting Mature Male Crabs								
New proposed	Low	0.2	9.404	9.865	34.374	97.521	1.94	4.07
New proposed	High	0.2	3.868	4.753	13.872	42.442	32.78	40.37
New proposed	Normal	0.0	7.267	8.085	23.694	69.373	11.75	23.01
New proposed	Normal	0.5	5.757	6.396	19.886	58.441	14.79	28.38
Depensatory S–R Curve and Harvest Rates Applied to Total Legal Crabs								
Status quo	Low	0.2	10.998	12.094	33.240	89.113	2.26	13.78
Status quo	High	0.2	1.942	3.401	7.039	22.962	63.97	69.56
Status quo	Normal	0.0	8.013	8.787	23.098	65.573	11.82	29.16
Status quo	Normal	0.5	5.847	6.427	18.003	52.570	18.76	36.51
Modif. status quo	Low	0.2	10.962	12.165	33.420	89.640	2.16	12.25
Modif. status quo	High	0.2	1.756	3.263	7.686	25.569	60.41	64.24
Modif. status quo	Normal	0.0	7.790	8.924	23.109	66.134	11.79	27.30
Modif. status quo	Normal	0.5	5.803	6.697	18.834	55.173	16.60	32.89
Depensatory S–R Curve and Harvest Rates Applied to Molting Mature Male Crabs								
New proposed	Low	0.2	9.334	9.812	34.117	96.845	1.94	4.05
New proposed	High	0.2	1.765	3.178	7.655	25.373	60.43	64.09
New proposed	Normal	0.0	7.060	7.942	23.123	67.870	11.77	23.19
New proposed	Normal	0.5	5.524	6.221	19.228	56.738	14.921	28.83

The modified status quo strategy is represented by a cut-off SP of 15,400 t, high harvest rate of 0.4 and low harvest rate of 0.2. "Cut-off" is a level of SP below which the low harvest rate is used and at or above which the high harvest rate is used.

harvest rate on new-shell, relatively young crabs because of fishery selectivity to meet market demands.

The proposed harvest strategy takes into account the relationship between shell condition and productivity levels of Tanner crab stocks. Strong year classes are dominated by new-shell crabs. Simulation results show that the proposed new strategy adjusts legal harvest rates according to recruitment strength, which is indexed by changes in shell condition. Contrary to the current harvest strategy based on legal male abundance only, use of mature crab abundance and shell condition gives the proposed new strategy a forward-looking feature. When an increase in future legal crab abundance is expected because of increased recruitment to the mature segment of the stock, legal harvest rates are increased. Conversely, during a downward recruitment cycle, reduced legal harvest rates will forestall the decline of large, old-shell males that are most virile (Stevens et al. 1993; Paul et al. 1995).

As a comparison to the status quo harvest strategy, the new approach had similar trade-off values between mean yield and variation in yield, but it led to fewer shortages of mates for mature females and reduced probability that population abundance falls below the overfished reference point over a long term. If reproduction can be limited because of a shortage of mature males, it is most likely during periods of low population abundance. As abun-

dance declines, spatial distribution becomes more patchy, thereby potentially reducing mating encounters. By incorporating a fishery threshold and stair-step harvest rates, the proposed new harvest strategy embodies a precautionary approach to fishery management (Restrepo et al. 1998). These features reduce mature harvest rates to protect reproductive potential during periods of low abundance when risks of overfishing or falling below the overfished reference point are high because of uncertainties in abundance estimates and population dynamics (i.e., depensation vs. compensation).

Although we did not explicitly evaluate economic impacts of the management alternatives, the proposed new strategy compares favorably to the current strategy. Slightly greater mean yield implies higher average gross revenues under the status quo as compared to the proposed strategy. However, the proposed strategy results in greater fishery stability, as indicated by lower variability in yield and more fishing opportunities because of fewer fishery closures. At low population abundance, catch expectations (preseason GHL) are much more indicative of actual harvests under the proposed new strategy than the status quo. Under the status quo harvest strategy, preseason GHL is set as 40% of legal male abundance, despite the fact that old-shell males predominate the population and that industry targets new-shell males, leading to more
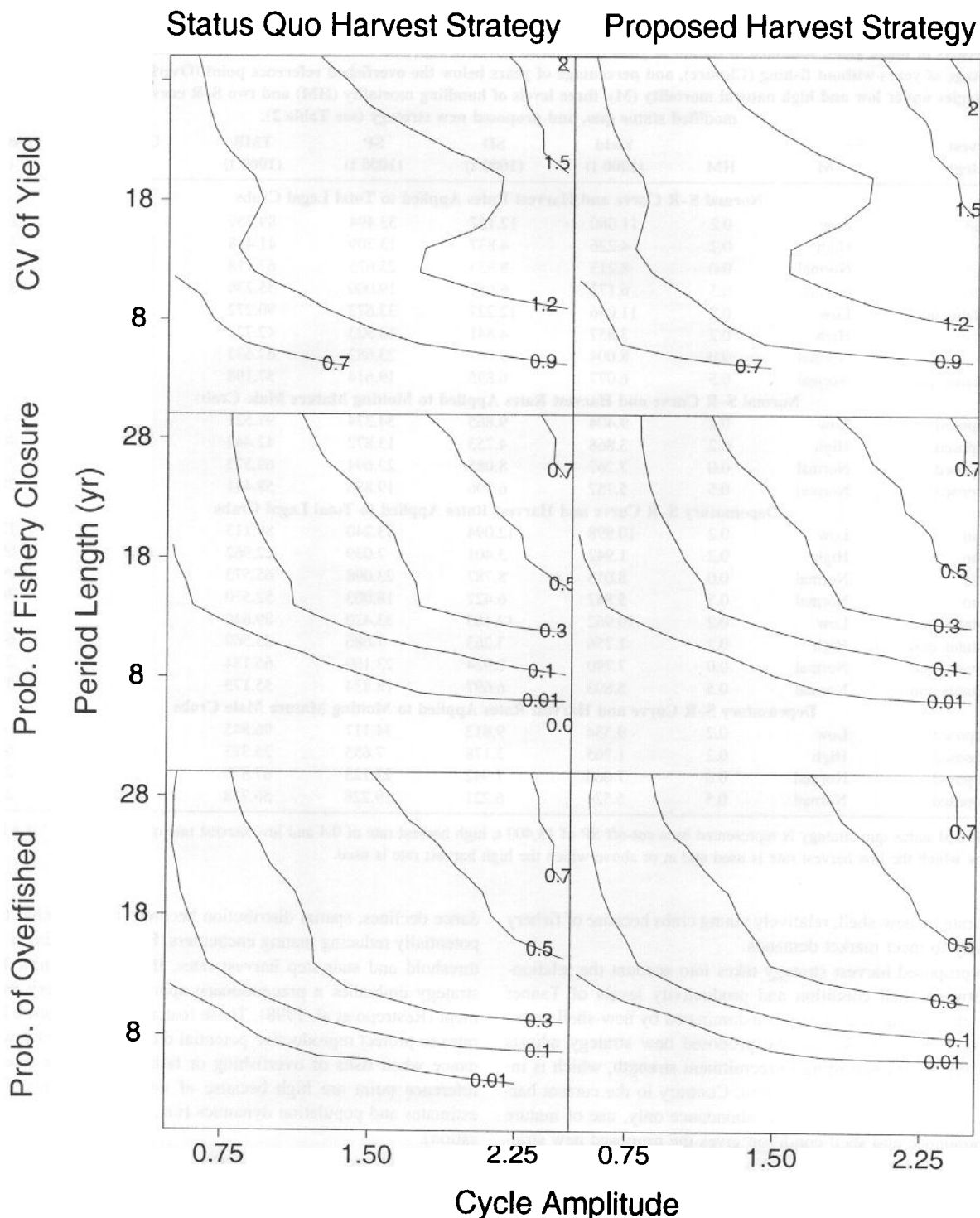
Figure 3. Contour plots of CV of yield, probability of fishery closure, and probability of total mature biomass below the overfished reference point by cycle amplitude and period length of the recruitment dynamics under the normal S–R curve for Bristol Bay Tanner crab. The plots are classified by the status quo harvest strategy and the proposed new strategy based on a 0, 10%, and 20% stair-step harvest rates of molting mature males.

grounds prospecting and catch sorting. As a result, low in-season catch-per-unit-effort triggers fishery closures short of the GHL as a conservation measure. Not only do inflated catch expectations depress prices, they may attract more fishery participants, thus reducing average revenues and increasing aggregate costs.

In our analysis of alternative harvest rate strategies, we attempted to consider total fishing mortality as the aggregate of landed catch, handling mortality of discards in the directed fishery, and bycatch mortality in ground fish and scallop fisheries. Landings are documented on transaction receipts between processors
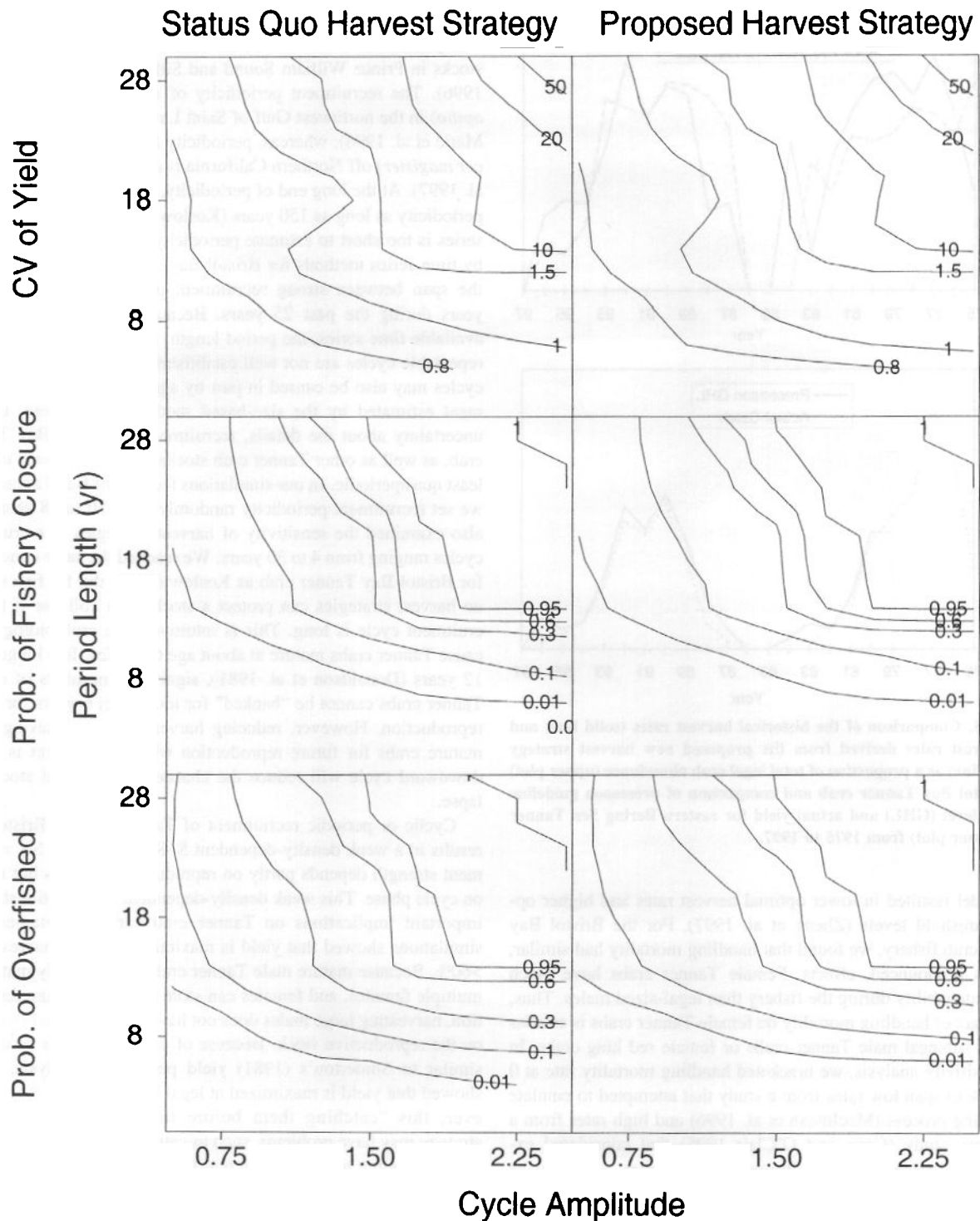
Figure 4. Contour plots of CV of yield, probability of fishery closure, and probability of total mature biomass below the overfished reference point by cycle amplitude and period length of the recruitment dynamics under the depensatory S-R curve for Bristol Bay Tanner crab. The plots are classified by the status quo harvest strategy and the proposed new strategy based on a 0, 10%, and 20% stair-step harvest rates of molting mature males.

and fishers called "fish tickets." At-sea observers monitor bycatch aboard vessels fishing for other species. Typically, total bycatch of Tanner crabs by ground fish and scallop fisheries is a small percentage of total crab abundance in the eastern Bering Sea. Whether a significant proportion of the Tanner crab population is adversely impacted by dredges and trawls, but not caught and observed, remains a matter of speculation. Large numbers of Tanner crabs are handled and discarded during crab fisheries because of restrictions on size, sex, season, and target species. In our study of the red king crab fishery in Bristol Bay, increased handling mortality in
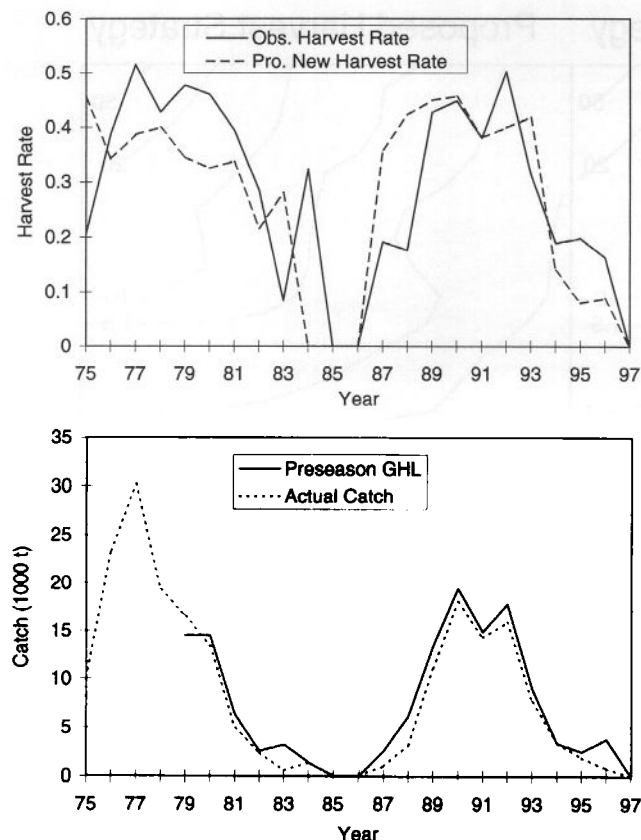
Figure 5. Comparison of the historical harvest rates (solid line) and the harvest rates derived from the proposed new harvest strategy (dotted line) as a proportion of total legal crab abundance (upper plot) for Bristol Bay Tanner crab and comparison of preseason guideline harvest level (GHL) and actual yield for eastern Bering Sea Tanner crab (lower plot) from 1975 to 1997.

our model resulted in lower optimal harvest rates and higher optimal threshold levels (Zheng et al. 1997). For the Bristol Bay Tanner crab fishery, we found that handling mortality had similar, but less pronounced, effects. Female Tanner crabs have much lower catchability during the fishery than legal-sized males. Thus, the impact of handling mortality on female Tanner crabs is smaller than on sublegal male Tanner crabs or female red king crabs. In our sensitivity analysis, we bracketed handling mortality rate at 0 and 50% to span low rates from a study that attempted to emulate the fishing process (MacIntosh et al. 1996) and high rates from a laboratory study (Carls and O'Clair 1995) that considered extremely cold air temperatures during winter fisheries. An extensive bibliography of capture and handling effects was compiled by Murphy and Kruse (1995) and reviewed in some detail by Zheng et al. (1997). Additional research is needed to assess handling mortality rates experienced by Tanner crabs accurately during commercial fisheries in the Bering Sea. Results from ongoing studies of cold wind chill effects (Kruse 1998) may significantly affect our estimates of handling mortality rate during winter fisheries. As this research is completed, the implications on crab fishery management need to be analyzed.

Recruitment cycles are the most striking feature of the population dynamics of Bristol Bay Tanner crab. Recruitment cycles are common to many fish and crab populations with typical periodicity of 10 to 26 years (Koslow 1989; Zheng and Kruse in press).

At the short end of periodicity, strong year classes occurred every four years from 1976 to 1988 for Pacific herring (*Clupea pallasi*) stocks in Prince William Sound and Sitka Sound, Alaska (Zheng 1996). The recruitment periodicity of snow crab (*Chionoecetes opilio*) in the northwest Gulf of Saint Lawrence is 8 years (Sainte-Marie et al. 1996); whereas, periodicity for Dungeness crab (*Cancer magister*) off Northern California is about 10 years (Higgins et al. 1997). At the long end of periodicity, some fish stock sizes had periodicity as long as 150 years (Koslow 1989). Although the time series is too short to estimate periodicity of the recruitment cycle by time series methods for Bristol Bay Tanner crab, it seems that the span between strong recruitment periods was about 13–14 years during the past 25 years. Because of the brevity of the available time series, the period length, and even the existence of repeatable cycles are not well established. The strong recruitment cycles may also be caused in part by age-class overlap in recruitment estimated by the size-based model. Nevertheless, despite uncertainty about the details, recruitment of Bristol Bay Tanner crab, as well as other Tanner crab stocks in Alaska, seems to be at least quasiperiodic. In our simulations for Bristol Bay Tanner crab, we set recruitment periodicity randomly from 10 to 18 years. We also examined the sensitivity of harvest strategies to recruitment cycles ranging from 4 to 30 years. We reached the same conclusion for Bristol Bay Tanner crab as Koslow (1989) did for fish stocks: no harvest strategies can protect a stock from collapse if the recruitment cycle is long. This is intuitive from crab biology. Because Tanner crabs mature at about age 6 and few live longer than 12 years (Donaldson et al. 1981), significant numbers of mature Tanner crabs cannot be "banked" for more than 6 years for future reproduction. However, reducing harvest rates and saving some mature crabs for future reproduction when recruitment is in the downward cycle will reduce the chance of prolonged stock collapse.

Cyclic or periodic recruitment of Tanner crab in Bristol Bay results in a weak density-dependent S–R relationship. So, recruitment strength depends partly on reproductive biomass but mostly on cycle phase. This weak density-dependent S–R relationship has important implications on Tanner crab harvest strategies. Our simulations showed that yield is maximized at legal harvest rates >60%. Because mature male Tanner crabs can annually mate with multiple females, and females can store sperm for future fertilization, harvesting large males does not have a proportional reduction on the reproductive stock. Because of this feature, our results are similar to Somerton's (1981) yield per recruit analysis, which showed that yield is maximized at legal harvest rates >70%. However, this "catching them before they die or are too old" strategy may have problems, such as causing insufficient males for mating, leading to recruitment overfishing, or depleting the reproductive stock to such a low level that depensation may occur. In the Gulf of Alaska, many depressed crab stocks have had extended periods of poor recruitment—red king stocks for >20 years and Tanner crab stocks for >10 years (Zheng and Kruse in press). The Alaska Board of Fisheries (a regulatory body making fisheries management policies for the State of Alaska) policy on king and Tanner crab management does not strive to maximize yield (ADF&G 1998). Instead, other objectives are considered, such as maintaining multiple size classes in the stock, maintaining sustained and reliable yields, and minimizing risks of irreversible adverse effects on reproductive potential. For Bristol Bay Tanner crab, the yield curve is relatively flat at high harvest rates, but much lower harvest rates can attain just slightly lower mean yields.

Compared to other alternative strategies we considered, our proposed new harvest strategy produces slightly lower mean yield, significantly lower variation in yield, it adjusts harvest rates according to stock productivity and creates more fishing opportunities while affording greater protection when the stock abundance is low. These features seem more consistent with the Board policy and provide a precautionary approach to fishery management.

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APPENDIX. POPULATION MODELS

Male Population Model

The abundances by carapace width (CW) and shell condition in any one year result from abundances the previous year minus catch and bycatch, handling, and natural mortality, plus recruitment and additions to or losses from each width class attributable to growth.

$$N_{m,l+1,t+1} = \sum_{l'=1}^{l'=l+1} \{P_{m,l',l+1}[(N_{m,l',t}e^{-Mm} - CN_{m,l',t}e^{(y-1)Mm})mn_{l',t}$$
$$+ (O_{m,l',t}e^{-Mm} - CO_{m,l',t}e^{(y-1)Mm})mo_t]\} + R_{m,l+1,t+1}$$
$$O_{m,l+1,t+1} = (N_{m,l',t}e^{-Mm} - CN_{m,l',t}e^{(y-1)Mm})(1 - mn_{l',t})$$
$$+ (O_{m,l',t}e^{-Mm} - CO_{m,l',t}e^{(y-1)Mm})(1 - mo_t) \qquad (A1)$$

where $N_{m,l,t}$ and $O_{m,l,t}$ are new- and old-shell male (m) crab abundances in width class l and year t, M_m is instantaneous natural mortality for male crabs, $mn_{l,t}$ and mo_t are molting probabilities for new-shell and old-shell crabs, $R_{m,l,t}$ is recruitment, y is lag in years between abundance assessment and the fishery, and $P_{m,l',l}$ is proportion of molting crabs growing from width l' to width l after one molt. $CN_{m,l,t}$ and $Co_{m,l,t}$ are combinations of bycatch mortality and catch (legal males) or bycatch and handling mortality (sublegal males) for new-shell and old-shell male crabs. Recruitment is defined as recruitment to the model and survey gear rather than recruitment to the fishery. We modeled male crabs $\geq$ 93 mm CW. $P_{m,l',l}$ is computed as follows.

Mean growth increment per molt is assumed to be a linear function of pre-molt width.

$$G_l = a + bl, \qquad (A2)$$

where a and b are constants. Growth increment per molt is assumed to follow a gamma distribution.

$$g(x|\alpha_l,\beta) = x^{\alpha_l-1}e^{-x/\beta}/(\beta^{\alpha_l}\Gamma(\alpha_l)), \qquad (A3)$$

The expected proportion of molting individuals growing from width class l_1 to width class l_2 after one molt is equal to the sum of probabilities with width range $[l_1, l_2)$ of the receiving width class l_2 at the beginning of next year; that is,

$$P_{m,l_1,l_2} = \int_{l_1-\iota}^{l_2-\iota} g(x|\alpha_l,\beta)dx \qquad (A4)$$

where ι is the mid-width of width class l_1.

Female Population Model

Major differences between the male and female population models are molting probability and fishing mortality. Upon maturity, female crabs stop molting and growing. Female crabs are not allowed to be retained in catch and are returned to the sea. The growth of immature females was modeled by functions similar to males [Eqs. (A2–4)]. Because females mature at smaller sizes than males, we modeled female crabs $\geq$ 70 mm CW.

New-shell females are either immature or primiparous (first-time spawners), and their abundance results from a combination of recruitment, growth, handling mortality, bycatch mortality, and natural mortality. Old-shell mature females are survivors of the mature females from the previous year:

$$N_{f,l+1,t+1} = \sum_{l'=1}^{l'=l+1} [P_{f,l',l+1}(N_{f,l',t}e^{-Mf} - CN_{f,l',t}e^{(y-1)Mf})(1 - mn_{l',t})]$$
$$+ R_{f,l+1,t+1}$$

$$O_{f,l+1,t+1} = (N_{f,l+1,t}e^{-Mf} - CN_{f,l+1,t}e^{(y-1)Mf})mn_{l+1,t} + (O_{f,l+1,t}e^{-Mf}$$
$$- CO_{f,l+1,t}e^{(y-1)Mf}) \qquad (A5)$$

where M_f is instantaneous natural mortality for female (f) crabs, $m_{l,t}$ is maturity probability for width class l and year, $R_{f,l,t}$ is recruitment, $CN_{f,l,t}$ and $CO_{f,l,t}$ are combinations of bycatch and handling mortality for new-shell and old-shell female crabs.

Catch, Bycatch Mortality, Handling Mortality, and Recruitment

Effective reproductive (or spawning) biomass was described in detail by Zheng and Kruse (1998). Annual effective reproductive biomass, SP_t, was estimated as

$$SP_t = \sum_l [(N_{f,l,t}nr_t + O_{f,l,t}or_t)W_l], \qquad \iota \geq 80 \text{ mm CW}$$
$$(A6)$$

where $N_{f,l,t}$ and $O_{f,l,t}$ is new-shell and old-shell female abundances in width class l and year t, W_l is mean weight of female crabs in width class l, ι is the mid-width of width class l, and nr_t or or_t are the ratios of male reproductive potentials TNM_t and TOM_t to new-shell and old-shell mature female abundances TNF_t and TOF_t ($\geq$80 mm CW) in year t or year $t - 1$, respectively; that is,

$$nr_t = TNM_t/TNF_t$$

$$or_t = \max[TOM_{t-1}/TOF_{t-1}, \qquad TOM_t/TOF_t] \qquad (A7)$$

Because female Tanner crabs can store sperm for subsequent fertilization, the ratios in year t-1 are also used. If nr_t or $or_t > 1$, we set them equal to 1; that is, there are sufficient mature males to mate with all mature females, and so the number of reproductive females is equal to the number of mature females. The male reproductive potentials for new-shell and old-shell mature females were defined as

$$TNM_t = \sum_l [(0.3N_{m,l,t} + O_{m,l,t}) nn_t],$$

$$113 \text{ mm} \leq \iota \leq 137 \text{ mm CW}$$

$$TOM_t = \sum_l [(0.1N_{m,l,t} + O_{m,l,t}) on_t], \qquad \iota \geq 113 \text{ mm CW} \quad (A8)$$

where $N_{m,l,t}$ and $O_{m,l,t}$ are mature male crab abundances in width class l and year t with new-shell and old-shell conditions, respectively, and nn_t and on_t are the maximum average number of new-shell and old-shell females mated by a matable male (old-shell mature males: 100%; new-shell mature males: 30% for primiparous females or 10% for multiparous females) in year t and are computed as follows.

$$nn_t = i + j (TNF_t - a1)/(a2 - a1) \text{ and } i \leq nn_t \leq i + j$$

$$on_t = i + j (TOF_t - b1)/(b2 - b1) \text{ and } i \leq on_t \leq i + j \quad (A9)$$

where $a1$ and $a2$ are the lowest and highest estimated mature new-shell female abundances (1.2 and 78.5 millions of crabs) from 1975 to 1997, $b1$ and $b2$ are the lowest and highest estimated old-shell mature female abundance (5.7 and 60.8 millions of crabs) during the same period (Zheng and Kruse 1998), and i and $i+j$ are the maximum average mates per matable male at the low and high female abundances. We assumed i to be 1 for both new-shell and old-shell females and j to be 4 for new-shell females and 2 for old-shell females (Zheng and Kruse 1998).

Annual effective reproductive biomass, SP_t, was used to determine whether the population is above threshold, T. If $SP_t \leq T$, then

no fishing is allowed; otherwise, the legal male harvest rate applied to exploitable legal crabs ($\iota \geq 138$ mm CW), EL_t, is

$$H_t = H L_t / EL_t \qquad \text{for 1st approach,}$$

$$H_t = H \qquad \text{for 2nd approach,}$$

$$H_t = \min[E(NM_t/EL_t) MH] \qquad \text{for 3rd approach,} \qquad \text{(A10)}$$

where H is legal harvest rate, L_t is total legal crab abundance, E is mature male harvest rate applied to NM_t, molting mature male abundance ($\iota \geq 113$ mm CW, 100% of new-shell crabs and 15% of old-shell crabs), and MH is the maximum allowable legal male harvest rate (50%). Catch by width from the directed fishery is equal to the product of exploitable legal harvest rate, legal male abundance, and selectivity ($sn_{m,t}$ for new-shell and $so_{m,t}$ for old-shell crabs),

$$CN'_{m,l,t} = H_t N_{m,l,t} sn_{m,l} \qquad \iota \geq 138 \text{ mm CW,}$$

$$CO'_{m,l,t} = H_t O_{m,l,t} so_{m,l} \qquad \iota \geq 138 \text{ mm CW,} \qquad \text{(A11)}$$

and total yield, TC_t, is obtained by multiplying by the corresponding weight and summing over all widths

$$TC_t = \sum_l [(CN'_{m,l,t} + CO'_{m,l,t})W_l], \qquad \iota \geq 138 \text{ mm CW} \qquad \text{(A12)}$$

Handling mortality is incorporated in the size-based model for female and sublegal male crabs. The number of deaths from handling mortality is a function of harvest rate, gear selectivity, and handling mortality rate (HM). Handling mortality for sublegal males is

$$PN_{m,l,t} = H_t N_{m,l,t} sn_{m,l} HM, \qquad 93 \leq \iota \leq 137 \text{ mm CW}$$

$$PO_{m,l,t} = H_t O_{m,l,t} so_{m,l} HM, \qquad 93 \leq \iota \leq 137 \text{ mm CW} \qquad \text{(A13)}$$

and handling mortality for females is

$$PN_{f,l,t} = H_t N_{f,l,t} sn_{f,l} HM, \qquad \iota \geq 70 \text{ mm CW}$$

$$PO_{f,l,t} = H_t O_{f,l,t} so_{f,l} HM, \qquad \iota \geq 70 \text{ mm CW} \qquad \text{(A14)}$$

To account for handling mortality of female crabs, effective reproductive biomass is updated after fishing by modifying Equation (A6) to deduct handling mortality from female abundance.

$$SP_t = \sum_l \{[(N_{f,l,t} - PN_{f,l,t}) nr_l + (O_{f,l,t} - PO_{f,l,t}) or_l]W_l\},$$
$$\iota \geq 80 \text{ mm CW} \qquad \text{(A15)}$$

Catch from the directed pot fishery, male handling mortality, and male bycatch mortality are combined for $CN_{m,l,t}$ and $CO_{m,l,t}$ in Equation (A1), and female handling mortality and bycatch mortality are summed for $CN_{f,l,t}$ and $CO_{f,l,t}$ in Equation (A5).

Recruitment is separated into a time-dependent variable, R_t, and size-dependent variables, $U_{m,l}$ and $U_{f,l}$, representing the proportion of male and female recruits belonging to each width class.

$$R_{m,l,t} = 0.55 R_t U_{m,l}$$
$$R_{f,l,t} = 0.45 R_t U_{f,l} \qquad \text{(A16)}$$

where $U_{m,l}$ and $U_{f,l}$ are described by gamma distributions similar to Equations (A3) and (A4) with two sets of parameters α_r and β_r. Annual recruitment is described by a normal Ricker S–R model.

$$R_t = SP_{t-k} e^{\alpha - \beta SP_{t-k} + v_t} \qquad \text{(A17)}$$

where k is recruitment age (8 years for males and 7 years for females), α and β are constants, and $v_t = \delta_t + A \sin(2\pi t/P)$ as environmental noise. δ_t was assumed as a $N(0,\sigma)$. We also assumed a depensatory S–R model as follows.

$$R_t = \kappa SP_{t-k}^{\theta} e^{v_t}, \qquad \text{when } SP_{t-k} \leq 6395t$$

$$R_t = SP_{t-k} e^{\alpha - \beta SP_{t-k} + v_t}, \qquad \text{when } SP_{t-k} > 6395t \qquad \text{(A18)}$$

where κ and θ are parameters.